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PAIRING CHRONOLOGY AND AGONISTIC BEHAVIORS OF WINTERING GREEN-WINGED TEAL AND MALLARDS

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ABSTRACT.—We examined pairing chronology and aggressive interactions of Green-winged Teal (*Anas crecca*) and Mallards (*A. platyrhynchos*) wintering in coastal Louisiana from October 1994 through March 1995. Many Mallards were apparently paired upon their arrival to coastal Louisiana in early November, as 11 of the first 20 females observed were paired. Most (≥90%) female Mallards were paired by mid-December. Green-winged Teal were first observed pairing in January and 81% of females observed during March were paired. For both Green-winged Teal ($P < 0.01$) and Mallards ($P < 0.01$) intraspecific aggressive conflicts were primarily won by individuals initiating encounters. Paired Green-winged Teal ($P < 0.05$) and paired Mallards ($P < 0.05$) typically won conflicts with unpaired conspecifics. In agonistic encounters between unpaired male and unpaired female Green-winged Teal, neither sex was dominant ($P > 0.05$). The frequency of aggressive interactions by paired and unpaired Green-winged Teal was similar ($P > 0.05$); in contrast, paired Mallards were less likely to participate in aggressive interactions than were unpaired Mallards ($P < 0.01$). Effects of pairing on aggressive interactions do not appear to be the same for Green-winged Teal and Mallards. *Received 5 Dec. 1997, accepted 21 April 1998.*

Waterfowl (Anatidae) are unique among migratory birds in forming pair-bonds on wintering areas and during migration (Rohwer and Anderson 1988). Female waterfowl likely benefit from winter pair-bonds because pairs dominate unpaired conspecifics and have improved access to food resources, and because males protect their paired females from harassment (Ashcroft 1976, Jorde et al. 1983, Paulus 1983). Conversely, the demands of female attendance and defense may elevate risks of injury, decrease foraging time, and increase energetic expenditures of males when they pair (Afton and Sayler 1982, Wishart 1983). Timing of pair formation, therefore, likely represents the compromise of female benefits and male costs, both of which probably vary among species and with habitats (Hepp and Hair 1983, Rohwer and Anderson 1988).

We examined the pairing behavior of Green-winged Teal (*Anas crecca*) and Mallards (*A. platyrhynchos*) wintering in coastal Louisiana, and collected information on their agonistic activities. Surprisingly few data exist concerning these subjects for wild Mallards in the Nearctic (e.g., Heitmeyer 1985, 1988).

METHODS

Study area.—Observations were made from October 1994 through March 1995 on the Atchafalaya River delta (29° 26′ N, 91° 20′ W), Saint Mary Parish, Louisiana. The Atchafalaya River delta is located in the eastern region of the Atchafalaya Bay and is a growing complex of shallow wetlands, mudflats, and low elevation islands (Johnson et al. 1985). Mudflats and islands are formed by natural accretion and by the pumping of dredge spoil. Daily tidal amplitude averages about 0.4 m, but it is a freshwater system. Surveys of waterfowl wintering on the delta are conducted 2–5 times a winter by Louisiana Dept. of Wildlife and Fisheries personnel. Peak survey estimates for winters 1988–1994 suggest 50,200 ± 10,600 (mean ± SE) ducks winter on the Atchafalaya River delta, the most common being Gadwall (*Anas strepera*), Green-winged Teal, and Mallards (M. R. Carloss, pers. comm.).

Observations.—We observed ducks from six elevated blinds located on mudflats adjacent to randomly chosen islands. We visited one or two blinds per day. To evenly distribute observations among mudflats we visited all six blinds in a rotation before we started another rotation. Order of visitation in each rotation was randomized. Most observations took place when tidal waters covered mudflats, because ducks were seldom near observation blinds when mudflats were exposed at low tide. Fog, particularly in late winter, limited observation hours.

We used focal individual sampling (Altmann 1974). We observed an individual bird for 5.5 min or until we lost it from view. We watched no more than one focal bird out of an individual flock during any 30 min period of the day. When Green-winged Teal and Mallards both occurred in a flock, we randomly determined which species to observe. Sex of focal individuals was randomly determined prior to observations.

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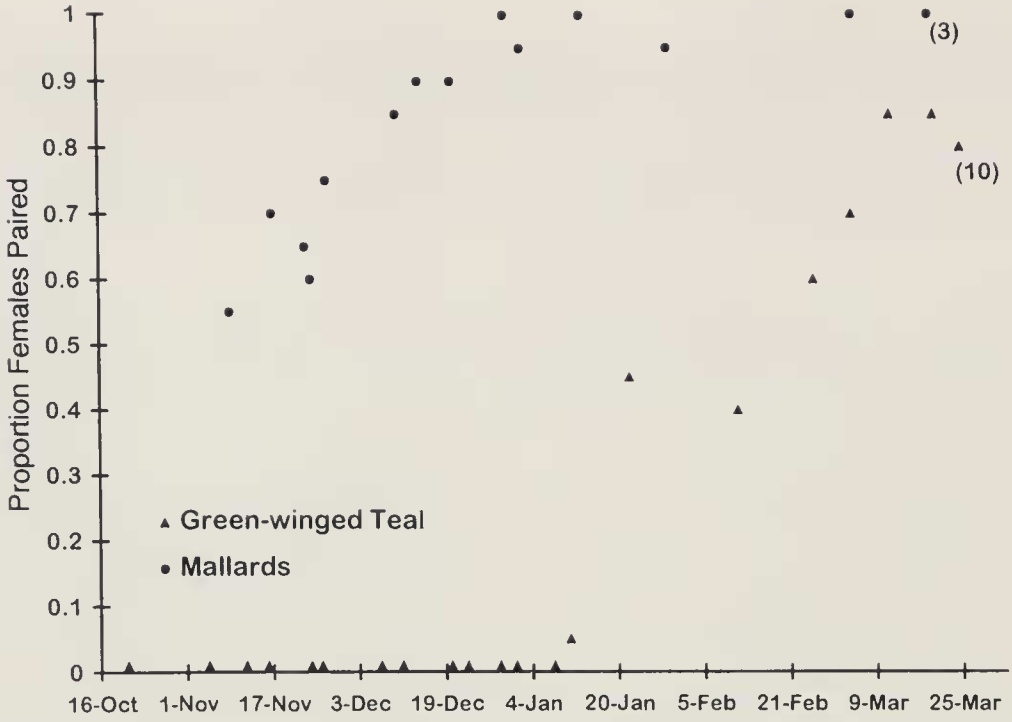

FIG. 1. Proportion of female Green-winged Teal and Mallards paired in coastal Louisiana. Each point represents 20 females unless indicated otherwise by a number in parenthesis. Sample sizes are 410 for Green-winged Teal and 263 for Mallards.

We chose focal individuals by scanning across a flock of birds, letting the spotting scope come to rest, then selecting the bird of predetermined sex and species closest to the center of the field of view (Lovvorn 1990). We recorded the pair status and aggressive interactions of focal birds. After an aggressive interaction we recorded species, sex, and pair status of the interacting bird.

The primary criterion used to determine pair status of focal individuals was sustained proximity to an individual of the opposite sex (Hepp and Hair 1983). Additionally, we used active association, such as coordination of activities or a male following a female, as indicators of pair status (Paulus 1983, Hepp and Hair 1983). By noting such criteria for a focal individual throughout the observation period, chance associations between unpaired male and female ducks were likely minimized (Weller 1965, Paulus 1983). Sex ratios of most waterfowl are male-biased (Bellrose et al. 1961, Johnson and Sargeant 1977), so we only considered females that were focal individuals when determining pairing chronology. Pair status of ducks that had aggressive interactions with focal individuals were not used in our analyses of pairing chronology because we could not observe these individuals over an extended time period to confirm their pair status.

Activities considered to be agonistic behaviors include: (1) fighting—interactions involving physical contact; (2) chasing—one bird rushing at another with no physical contact occurring; and (3) bill threats—open-beak display in the direction of another bird (Paulus 1983, Hepp and Hair 1984). Supplanting, a low-level conflict that occurs when a bird moves away from an advancing individual without a confrontation (Patterson 1982), was observed during focal sampling, but not recorded or analyzed. Supplanting is difficult to detect consistently because it involves subjective interpretation of bird movements (see also Paulus 1983).

We used χ^2 tests (Freund and Wilson 1993) to analyze frequency data concerning agonistic behaviors, and limited these data to observations lasting at least 2 min. Statistical calculations were performed on an IBM compatible personal computer using SAS (PROC FREQ, SAS Institute Inc. 1990). When investigating whether males or females were differentially involved in aggressive interactions we adjusted for skews in population sex ratio. To correct the expected frequencies we multiplied the observed numbers by the sex ratio of the local population (Hepp and Hair 1984). We obtained sex ratio data by counting males and females in a flock before focal observations began and then averaging the sex ratio per flock for the period of interest. Sex ratio information was recorded only for Mallards.

RESULTS

Pairing chronology.—Large numbers of Green-winged Teal arrived on the study area in early October, but courtship and pairing activities were not observed until late December. Paired female Green-winged Teal were first observed during the second week of January (Fig. 1), and the fraction of teal that were paired increased steadily during late winter. During March, the last month in which observations were made, 81% of females (n =

TABLE 1. Distribution of intraspecific agonistic encounters among Mallards[a] at the Atchafalaya River delta, Louisiana.

	Observed frequencies	Expected frequencies[b]	χ^2
Male	76	52.9	10.05
Female	22	45.1	11.82
Total	98	98	21.87[c]

[a] Paired and unpaired.
[b] Based on male : female ratio of 54:46. Calculations of expected frequencies follow Hepp and Hair (1984): (total number of observations) × (percentage of sex in population).
[c] df = 1, $P < 0.05$.

TABLE 2. Distribution of intra- and intersexual agonistic behaviors by Mallards at the Atchafalaya River delta, Louisiana.

Aggressor → interaction bird	Observed frequencies	Expected frequencies[a]	χ^2
Male → Male	32	20.5	6.42
Male → Female	6	17.5	7.54
Total male initiated conflicts	38	38	13.96[b]
Female → Female	5	5.9	0.15
Female → Male	6	5.1	0.17
Total female initiated conflicts	11	11	0.32[c]

[a] Based on a male : female ratio of 54:46. Calculations of expected frequencies follow Hepp and Hair (1984): (total number of observations) × (percentage of second sex in population).
[b] df = 1, $P < 0.05$.
[c] df = 1, $P > 0.05$.

62) were paired. Few Green-winged Teal remained on the study area in late March.

We observed few Mallards on the study site before 2 Nov. 1994, and we collected no data on Mallards before this date. Many Mallards apparently were paired when they arrived on the study area, as 55% of females (n = 20) observed before 9 Nov. 1994 were paired. The percent of paired females increased rapidly and stabilized near 95% during late December (Fig. 1). By March, most Mallards had left the study area.

Sex ratios. — The average sex ratio (males: females ± SE) of Mallard flocks (n = 488 flocks) during the study period was 1.17:1 ± 0.83. Sex ratios in November were 1.27:1 ± 1.90 (n = 174); in December were 1.27:1 ± 1.16 (n = 176); in January were 1.04:1 ± 0.96 (n = 93); in February were 1.08:1 ± 1.58 (n = 32); and in March were 1.00:1 ± 0.00 (n = 13). Flock size of Mallards was small, averaging 3.0 ± 0.12 (SE) birds per flock. Fifty-eight percent of flocks containing Mallards had only one pair; flocks of six or fewer Mallards typically (77%) contained an even number of males and females.

Agonistic behaviors.—Green-winged Teal (n = 792) were observed for 69.4 h. Intraspecific aggressive interactions with clear outcomes (84 of 85) overwhelmingly were won (99%) by the Green-winged Teal initiating the encounter (χ^2 = 72.4, df 1, $P < 0.01$). Among unpaired Green-winged Teal, neither males (n = 11) nor females (n = 19) were more likely to win intersexual encounters (χ^2 = 2.13, df 1, $P > 0.05$). Paired Green-winged Teal won 83% (n = 12) of their aggressive interactions with unpaired teal (χ^2 = 5.33, df = 1, $P < 0.05$). One unpaired male drove away two pairs and was responsible for both conflicts won by unpaired birds. Pair status did not influence a Green-winged Teal's likelihood of being involved in a conflict; the frequencies of aggressive interactions among unpaired (63 of 638 individuals observed) and paired (8 of 154 individuals observed) focal birds were not different (χ^2 = 2.86, df 1, $P > 0.05$).

Focal Mallards (n = 523) were observed for 46.6 h. Considering unpaired and paired Mallards together, males were more likely to engage in agonistic behaviors than were females (Table 1). For males, agonistic encounters were skewed significantly toward interactions with other males, but females were likely to interact with either males or other females (Table 2). Intraspecific aggressive interactions with clear outcomes (43 of 49) were typically won (88%) by the bird initiating the encounter (χ^2 = 42.3, df 1, $P < 0.01$). We observed only seven interactions between male and female Mallards of the same pair status, so we did not test to see if one sex was dominant. Paired Mallards were dominant to unpaired Mallards, winning 79% (n = 14) of the aggressive interactions that occurred between them (χ^2 = 4.57, df 1, $P < 0.05$). Pair status influenced a Mallard's likelihood of being involved in a conflict; the frequency of aggressive interactions among unpaired (20 of 121 individuals observed) and paired (11 of 402 individuals observed) focal birds differed (χ^2 = 26.4, df 1, $P < 0.01$). Unpaired focal male Mallards were more likely (16 of 77 individuals ob-

served) than paired focal males (5 of 185 individuals observed) to participate in agonistic activities ($\chi^2 = 19.3$, df 1, $P < 0.01$). However, unpaired focal Mallard females did not participate in more agonistic interactions (4 of 44 individuals observed) than paired focal females (6 of 217 individuals observed; $\chi^2 = 3.54$, df 1, $P > 0.05$).

Green-winged Teal did not initiate any interspecific aggressive interactions. They lost conflicts with Gadwall ($n = 2$), Blue-winged Teal (*Anas discors*; $n = 1$), Northern Pintail (*A. acuta*; $n = 1$), and Northern Shoveler (*A. clypeata*; $n = 1$). Mallards were involved in seven interspecific aggressive interactions. Mallards won conflicts with Gadwall ($n = 1$) and American Coots (*Fulica americana*; $n = 2$), but lost one conflict with a Canvasback (*Aythya valisineria*) and two of three conflicts with Mottled Ducks (*Anas fulvigula*).

DISCUSSION

Female Mallards wintering in coastal Louisiana may pair earlier and in higher proportions than Mallards wintering in Missouri (Heitmeyer 1988). In Missouri, approximately 57% of female Mallards were paired during November and 85% were paired during March (Heitmeyer 1988). In contrast, 65% of females were paired during November and 95% or more were paired from January onward in our study.

Mallards wintering in Missouri and coastal Louisiana may pair at different times because of differences in habitat. Milder conditions in Louisiana may allow Mallards to devote energy to courtship and pair maintenance earlier in the season (Afton and Sayler 1982, Baldassarre and Bolen 1986). This suggestion is made cautiously, because many of the first arriving Mallards on our study site appeared to be paired. Furthermore, the small average flock size we observed may reflect spatial separation of paired Mallards from larger flocks of unpaired birds, which were rare on our study area. During winter, paired ducks tend to use different habitats than unpaired ducks (Paulus 1983, Heitmeyer 1985), and pairs frequently occur in small groups that are segregated from unpaired ducks (Heitmeyer 1985, Paulus 1988). Spatial separation of pairs from large flocks may minimize the risks of splitting pair-bonds and the concomitant loss of time and energy spent pairing (Paulus 1988). Thus, the early pairing rates we observed for Mallards might not reflect an actual difference in timing of pair formation per se, but rather a difference in the distribution of paired versus unpaired Mallards in our region or throughout their winter range.

Pairing chronology of Green-winged Teal in the Atchafalaya River delta is quite similar to that of teal wintering in coastal North Carolina (Hepp and Hair 1983). Surprisingly, Rave and Baldassarre (1989) found later pairing dates for Green-winged Teal in coastal southwest Louisiana, where only 7% of females were paired during January and only 59% were paired during March. The similarity of pairing times for Green-winged Teal in North Carolina (Hepp and Hair 1983) and in this study confounds any attempt to explain timing differences among studies based on location or habitat type.

Although differences in pairing times among studies, for both Green-winged Teal and Mallards, might represent temporal effects, we do not believe they reflect differences in assigning pairing chronology. The studies that we cited concerning pairing chronology (i.e., Hepp and Hair 1983, Heitmeyer 1988, Rave and Baldassarre 1989, this study) used similar criteria to assign pair status.

Paired ducks are dominant to unpaired conspecifics (Jorde et al. 1983, Hepp and Hair 1984). Earlier literature (e.g., Jorde et al. 1983, Paulus 1983, Hepp and Hair 1984, Heitmeyer 1985) also suggests that unpaired male dabbling ducks dominate unpaired females. Our data on Green-winged Teal do not support this generalization; females won 63% of their encounters with males. Other cases where males do not dominate females include Mottled Ducks in Louisiana (Paulus 1988) and Blue-winged Teal, Northern Pintails, and Northern Shovelers wintering in southern Mexico (Thompson and Baldassarre 1992). Even if males are not dominant, there should be benefits to females for establishing pairs. Males are vigilant and provide their mates with protection from conspecific harassment (Ashcroft 1976, Rohwer and Anderson 1988).

Dominance of pairs, which is well established (Jorde et al. 1983; Paulus 1983, 1988; Hepp and Hair 1984; Heitmeyer 1985), may reflect early pairing of dominant individuals or may be a result of the pair-bond (Patterson

1982, Wishart 1983, Hepp 1989, Sorenson and Derrickson 1994). Green-winged Teal and Mallard pairs dominated unpaired birds and participated in fewer aggressive interactions than unpaired birds, although the second effect was not significant in Green-winged Teal.

Future studies that focus on the costs and benefits of pairing for males and females would aid our understanding of the relationships between pairing chronology, aggression, and habitats. Further research also is needed on the distribution of paired and unpaired Mallards during early winter. Information gained through such an effort might change the way degradation or loss of wetlands are viewed in areas now considered to be of secondary importance to Mallards.

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